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ENVIRONMENTAL AND SEXUAL DIMORPHISM IN CREPIDULA.

BY EDWIN G. CONKLIN, PH. D.

I. The genus *Crepidula* Lam. is represented on our North Atlantic Coast by at least three species, viz. : *C. fornicata* Lam., *C. plana* Say, and *C. convexa* Say, while the species *C. adunca* Sby. and *C. navicelloides* are abundant on the Pacific Coast of the United States.

All these species are more or less completely sedentary, and they are usually, though not invariably, carried about by other animals with whom they are messmates and upon whom they are securely fixed. All the larger species of *Crepidula* are immovably fixed to one spot, e. g., *C. fornicata*, *C. plana*, *C. navicelloides*, while the smaller species *C. convexa* and *C. adunca* are able to move about to a limited extent.

Among these smaller forms the characters of the shell are fairly constant, but among the larger forms it is well-nigh impossible to tell what the normal or usual form is; this is especially the case with *C. plana*, where it is a rare thing to find two shells alike.

Even among the smaller species there are marked local varieties depending upon the immediate environment, e. g., *C. convexa* as found on *Illyonassa* and *Littorina* shells is deeply convex and very darkly pigmented. On oyster shells it is very much flatter and lighter in color, and is frequently mottled as shown in Plate XXI, Row 2. This local variety has been considered a distinct species, viz. : *C. glauca* Say; its anatomical and embryological characters show, however, that it is not specifically distinct from *C. convexa*. The same is true of Lea's species, *C. acuta*, which is merely a local form of *C. convexa*.

Among the larger and more sedentary species, *C. fornicata* and *C. plana*, the most remarkable differences in the shape of the shells may be observed due to the character of the surface upon which they are attached. "Upon a smooth, plane surface, the shell is regular and unusually broad and flat; on a convex surface it is deep and highly arched; on a concave surface it is concave; on a twisted surface, such as the columella of *Neverita*, it is twisted; on an irregular surface, such as a rough stone, it is irregular; if pressed upon from the sides,

the animal and shell become long and narrow; if growth is limited in front, the shell becomes short and broad; if limited on all sides, the shell may increase greatly in thickness but remains small in area, completely filling the space in which it is found. In such cases, the lines of growth are crowded close together, and the very edge of the shell may be as thick as any other portion.

"The cause of these variations is not far to seek; the shape of the shell is conditioned by the shape and position of the mantle edge; the mantle is moulded over the surface upon which the animal rests; and consequently the shape of the shell comes to correspond in time to any sort of a surface upon which the animal is attached."¹

Arnold Graf² has described a case in which a shell of *C. fornicata* was marked by radial folds corresponding to those of a *Pecten* upon which the *Crepidula* was attached. I have, myself, repeatedly noticed similar cases.

More recently, Bradley B. Griffin,³ has called attention to a *Placuanomia* shell which was found attached to a valve of *Saxidomus*, and which was marked by lines and folds exactly coinciding with the concentric markings of the *Saxidomus*.

Griffin also remarks that many similar phenomena have been observed and commented upon by paleontologists in fossil shells, and he refers particularly to two papers by Keyes⁴ on the modifications of *Platyceras* shells due to the surface of attachment.

All these modifications are similar to those which I have observed in *Crepidula*, and are, undoubtedly, due to the causes which have been mentioned.

Such irregularities of form could scarcely be called dimorphism, though they might properly enough be called environmental polymorphism. In no case which I have observed is there any evidence that any of these modifications of form are becoming hereditarily fixed, though they may be found in many individuals and have frequently been considered of specific value (e. g., *Crepidula glauca* and *C. acuta*).

¹ Conklin, The Embryology of *Crepidula*. Jour. Morph., Vol. XIII, 1897.

² A. Graf, Adaptation of the shells of *Crepidula fornicata* to the shell of *Pecten jacobus*. Trans. New York Academy of Sciences, April 3, 1896.

³ Griffin, Adaptation of the shell of *Placuanomia* to that of *Saxidomus* with remarks on shell adaptation in general. Trans. New York Academy of Sciences, Feb. 22, 1897.

⁴ Keyes, The Sedentary Habits of *Platyceras*, Am. Jour. of Science, October, 1888, and On the Attachment of *Platyceras* to Palaeocrinoids and its effects in modifying the forms of the Shell, Proc. Am. Phil. Soc., Vol. XXV, 1888.

II. An interesting case of environmental dimorphism to which I wish to call attention is found in a race of dwarfs which is specifically identical with *C. plana* (Plate XXII, Rows 3 and 4).

This species is found most abundantly inside dead shells of *Neverita* inhabited by the large hermit crab, *Eupagurus Bernhardus*. In this position individuals grow to a large size, mature females frequently reaching a length of 2 inches and a breadth of $1\frac{1}{4}$ inches. On the other hand, the dwarfs referred to are found within dead shells of *Illyonassa* or *Littorina* inhabited by the little hermit, *Eupagurus longicarpus*, and never exceed $\frac{3}{4}$ inch in length by $\frac{3}{8}$ in breadth, i. e., they are about $\frac{1}{3}$ the linear dimensions of the larger form. I removed from their shells a large number of individuals of both the common and the dwarfed forms, and estimated the volume of the body in the following way: The individuals were first placed on blotting paper to remove any excess of water, and then a given number were dropped into a known volume of water in a finely graduated tube. In this way the average body volume could be determined with sufficient accuracy. The results of very many such measurements in which mature females of all sizes were taken without any conscious selection of large or small individuals show that the average body volume of a mature female of *C. plana* is $\frac{3}{4}$ cc., while the average volume of a mature female of the dwarf variety is $\frac{1}{10}$ cc., i. e., the average body volume of the typical form is about thirteen times that of the dwarf. This disproportion in size would be much greater if comparison were made between the largest individuals obtainable in the two classes since the dwarfs are much more uniform in size than the type forms.

This difference in size is not due merely to differences in the age of individuals compared, since only sexually mature females were chosen for purposes of measurement; all the individuals measured were carrying egg masses, and unless we assume that sexual maturity appears much earlier in the dwarfs than in the giants, we must conclude that they were of approximately the same age. A careful study of the shells of the dwarfs and giants also strengthens the view that the former are, on the whole, as old as the latter; for while the dwarf shells are much smaller and more delicate than those of the giants, they are, in no sense, immature in shape or character; the lines of growth are closely crowded together, the margin of the shell is frequently thickened, and its general shape differs from that of an immature shell.

The dwarfs are perfectly formed in all respects, and all organs of the body seem to be reduced in size in about the same proportion.⁵ Strangely enough, however, the cells composing the various organs of the dwarfs are not reduced in size. It must follow, therefore, that a smaller *number* of cells are present in the various organs and also in the entire body of the dwarf than in the giant. It is an almost impossible task to count the actual number of cells present, even in a very small organ. I have, however, been able to count the number of cells in a cross section of the rectum, and while the size of the cells here, as everywhere, is the same in both varieties, the number of the cells in the sections is greater in the giants than in the dwarfs. Of all the cells of the body the ova are most readily enumerated; they are laid in capsules which can be easily counted, and each of which contains a nearly constant number of eggs. Oft repeated observations show that, without exception, the fertilized but unsegmented eggs of the dwarfs are of exactly the same size as those of the giants, but are very much fewer in number; e. g., the following table of averages has been obtained from a large number of observations:—

| | Diam. of egg. | No. of caps. | Eggs in caps. | Total No. |
|-------------------------|---------------|--------------|---------------|-----------|
| <i>C. plana</i> (type) | .136 mm. | 51 | 176 | 9,000 |
| <i>C. plana</i> (dwarf) | .136 mm. | 48 | 64 | 3,070 |

It is notable that the number of capsules formed is nearly the same in the two varieties, though there is a great difference in the number of eggs inclosed in each capsule.

In *Crepidula*, therefore, the cell size is constant, and variations in the size of the body are due to variations in the number of cells present.

This conclusion leads naturally to an inquiry as to the cause of the smaller number of cells, and hence the smaller size of the body of the dwarfs as compared with the giants. In this connection it will be remembered that Semper⁶ long ago observed that the pond

⁵ It is worthy of note that certain organs, particularly the gill filaments, are reduced in *number* in the smaller individuals but not in size, e. g., the numbers of gill filaments in three different individuals were as follows:—

| | | |
|-----------------|-------|---|
| Mature female | . . . | Vol. of body, .75 cc., Gill filaments, 204. |
| Immature female | . . . | Vol. of body, .05 cc., Gill filaments, 53. |
| Dwarf female | . . . | Vol. of body, .05 cc., Gill filaments, 58. |

⁶ Semper, Ueber die Wachstumsbedingungen der *Linnaeus tagnalis*. Arb. aus dem. Zool. Zoot. Inst. Würzburg, Vol. I, 1874, also Animal Life as affected by the Natural Conditions of Existence, 1879.

snail (*Limnæa stagnalis*) remained small when grown in a small quantity of water, while the larger the quantity of water, up to 4,000 or 5,000 cc., the larger the snails reared in it. As the result of numerous experiments, Semper concluded that this difference in size was not due to differences in the quantity of food, inorganic salts or oxygen obtainable, and he suggested that some unknown substance must be present in the water which acts as a stimulus to growth without actually contributing to it.

More recently, DeVarigny⁷ has repeated these observations, and concludes, as the result of several experiments, that the relative volume of the water, in which the snails are grown, is much less important than the relative amount of surface exposed. He holds that the larger the surface the more exercise the animals are able to take, and, therefore, the larger they become. His results show that Semper's conclusions are untenable, but they by no means establish his own. It is certainly not generally true, as he holds, that physiological or mechanical impedimenta to movement result in dwarfing. The larger forms of *C. plana* are as immovably fixed as the dwarfs; in this case, therefore, movement can have nothing to do with body-size.

In *Crepidula*, the dwarfed form is unquestionably correlated with the smaller size of the shell in which it has found lodgement. It is possible that the diminished size is due to diminished supply of food or oxygen; however, the following observation is opposed to this view: I have never found more than one mature female in a shell inhabited by the small hermit, whereas, from four to eight very large individuals may be found in the shell of a large hermit; under these circumstances, it seems very improbable that the difference in size is due to differences in the amount of food or oxygen obtainable. The most natural interpretation is that the dwarfing is due to pressure which limits growth in various directions; though it must be confessed that the shell of the dwarf remains thin and delicate, whereas, the shells of the common form which are limited in growth by surrounding hard parts grow thick and have a distorted appearance. The fact, also, that the males of all these species, and especially of *C. plana*, remain very much smaller than the females (as is pointed out in Section III), speaks against the view that the smaller size is due to a diminution of food or oxygen, since the males have

⁷ DeVarigny, *Experimental Evolution*, 1891.

the same opportunities in this regard as the much larger females; and the fact that the males are in no case limited for space in which to grow, as are the females, makes against the view that their small size, as compared with the females, is due to pressure. On the whole, it seems to me, that some factor, other than those mentioned, is involved.

Whatever the cause of the dwarfed form, it will be noted that in *Crepidula* it operates by stopping cell-growth and division, and the real causes of so fundamental a phenomenon are worthy of a more extended study than I have, as yet, been able to devote to it.

There is good evidence that these dwarfs are not a permanent variety or race. In the first place there are no anatomical differences between the two varieties save size only; secondly, the eggs, embryos and larvæ of the two cannot be distinguished; thirdly, there is evidence that the dwarfs do not produce enough eggs to continue the variety in its present numbers, for since the type and rate of development are the same in the two varieties, it is probable that relatively no more individuals will come to maturity in the one case than in the other, and yet every giant female produces three times as many ova as are produced by a dwarf; the relative number of these two varieties remains practically constant from year to year, and, therefore, I think it must follow that the ranks of the dwarfs are continually recruited from the descendants of the giants. Both live together on the same beach under about the same conditions of food, temperature and water, the embryonic and larval development of both forms are identical, and it seems probable that the adults of both would be the same if one was not forced by the smaller quarters which it inhabits to remain smaller than the other. But what is still more conclusive is the following observation: A few specimens were found which showed by the shape and character of their shells that at one time they had been typical dwarfs; afterward, having been detached, they obtained a new foothold on a larger surface, and their shells increased in size, the new portions of the shell becoming shaped so as to fit the surface upon which they had found a new home. In every such shell one can recognize both the dwarf and the normal forms. The dwarfs are what they are by reason of external conditions, and not because of inheritance; they are, in short, a physiological and not a morphological variety. In such a case the shape and size of the body, as well as the number of cells in the entire organism, are greatly modified by the direct action of

environment. But in this case, as in that of the irregular shells mentioned above, I have found no evidence that these modifications have become in the least degree heritable.

III. Marked as is the environmental dimorphism in *C. plana*, the sexual dimorphism is even greater. The average body volume of a mature male of this species is about $\frac{1}{2}$ cc., while the volume of an adult female is about $\frac{2}{3}$ cc.; that is, the average female is almost 15 times as large as the average male. In all species of *Crepidula* the males are smaller than the females, though the difference in size is greatest in *C. plana*. The following table gives the actual and relative sizes of males and females of the different species:—

| Species | Actual vol. of body. | | Relative vol. of body. | |
|-------------------------|----------------------|----------|------------------------|---------|
| | Male. | Female. | Male. | Female. |
| <i>C. plana</i> , . . | .046 cc. | .667 cc. | 1. | 14.5 |
| <i>C. adunca</i> , . . | .025 cc. | .208 cc. | 1. | 8.3 |
| <i>C. convexa</i> , . . | .01 cc. | .05 cc. | 1. | 5.0 |
| <i>C. fornicata</i> , . | 1.25 cc. | 1.6 cc. | 1. | 1.34 |

These averages are derived from the measurement of at least 20 mature individuals of each sex.

In the case of the males as in that of the dwarfs, the smaller size of the body is due to the smaller number of cells present rather than to the smaller size of the cells. Careful measurements of cells of the intestine, stomach, liver, kidney, muscles of foot, epithelium of gill chamber, and epithelium of gill filaments show that the cell size remains the same in the male as in the female. Whatever the ultimate cause of the smaller size of the males may be, it operates in this case as in that of the dwarfs by causing a cessation of cell growth and division.

In all these species the males are almost invariably found mounted upon the shells of the females, and in *plana*, *adunca* and *convexa* they are able to move about more or less freely, but the full-sized males of *fornicata* are as immovably fixed to one spot as are the females. In such cases sexual union could take place only between individuals attached near to each other. On muddy bottoms *C. fornicata* has the habit of piling together, one individual on top of another, until there may be as many as ten or twelve individuals in a single chain; such chains are often found in which there is not a single male, and yet I have never found an unfertilized female. Again, perfectly isolated females with large numbers of fertilized

eggs are of frequent occurrence. In such cases I was, for a long time, puzzled to know how the eggs came to be fertilized. I afterward found by a study of serial sections that in the females of all the species there is a seminal receptacle in the form of a convoluted tubule which opens into the oviduct, and in all mature individuals this is filled with spermatozoa. These spermatozoa are attached by their apices to the walls of the receptacle; it is probable that they receive nutriment from these walls just as they do in the seminiferous tubules of the male, and that they can live indefinitely in this position. Since there are myriads of these spermatozoa in the receptacle, and since they are carefully conserved, as is shown by the facts that polyspermy rarely, if ever, occurs, and that no superfluous spermatozoa are found in the egg capsules or oviduct, it might well be that one sexual union would suffice for a life time. In some such way as this must be explained the fact that perfectly isolated females of *C. fornicata* lay eggs which are always fertilized, though both the full grown males and females of this species are perfectly sedentary.

In the case of the other species named, the males are never immovably fixed to one spot, they are able to move about slowly upon the surface of attachment, and, if detached, can obtain a new foothold; their shells, also, are not distorted so as to fit irregular surfaces as is the case with the females. In all cases locomotion is limited to small individuals. The young of all species and of both sexes crawl about freely and rapidly. In *C. convexa* individuals of both sexes retain this power to a limited extent, but the large females of *adunca*, *navicelloides* and *plana* become firmly fixed, whereas the males of these species remain relatively small and retain, to a certain extent, their power of locomotion. The larger any individual becomes, the more limited are its powers of movement, and it is evidently in relation to this fact that the males are so much smaller than the females; because of this marked sexual dimorphism, the large and sedentary females may be repeatedly, or, in *C. fornicata*, perhaps once for all, visited and fertilized by the smaller and motile males.

In *C. plana* the shell of the male is more nearly round than that of the female, and is usually sharply pointed at the apex; it is thicker than an immature shell, the edges being thickened and the lines of growth crowded together as is the case with the dwarfs. These characters are so constant that it is usually easy to distinguish a

male from an immature female, as is shown in Plate XXIII, where immature individuals are shown in the first row, mature males in the second, and an immature female at the right end of the third row. To the left of this immature female are shown a number of individuals in which the older part of the shell has the male characters, while the newer part has those of the female. "In such animals the penis is usually very small, and, in some cases, has almost entirely disappeared. Quite a complete series of stages in the degeneration of this organ was observed, from the fully-formed organ on the one hand, to a minute papilla on the other. Sections of such animals show that neither male nor female sexual cells are produced at this time. The evidence seems to favor the view that we have, in these cases, an example of proterandric hermaphroditism, but I am not able to assert that this is really the case, although I have spent much time in attempting to decide it."⁸ Further, I have not studied a sufficient number of cases to be able to decide whether this is a regularly occurring phenomenon or only an unusual and abnormal approach to hermaphroditism.

EXPLANATION OF PLATES.

The plates are from photographs of actual specimens, and are reduced about one-third in size.

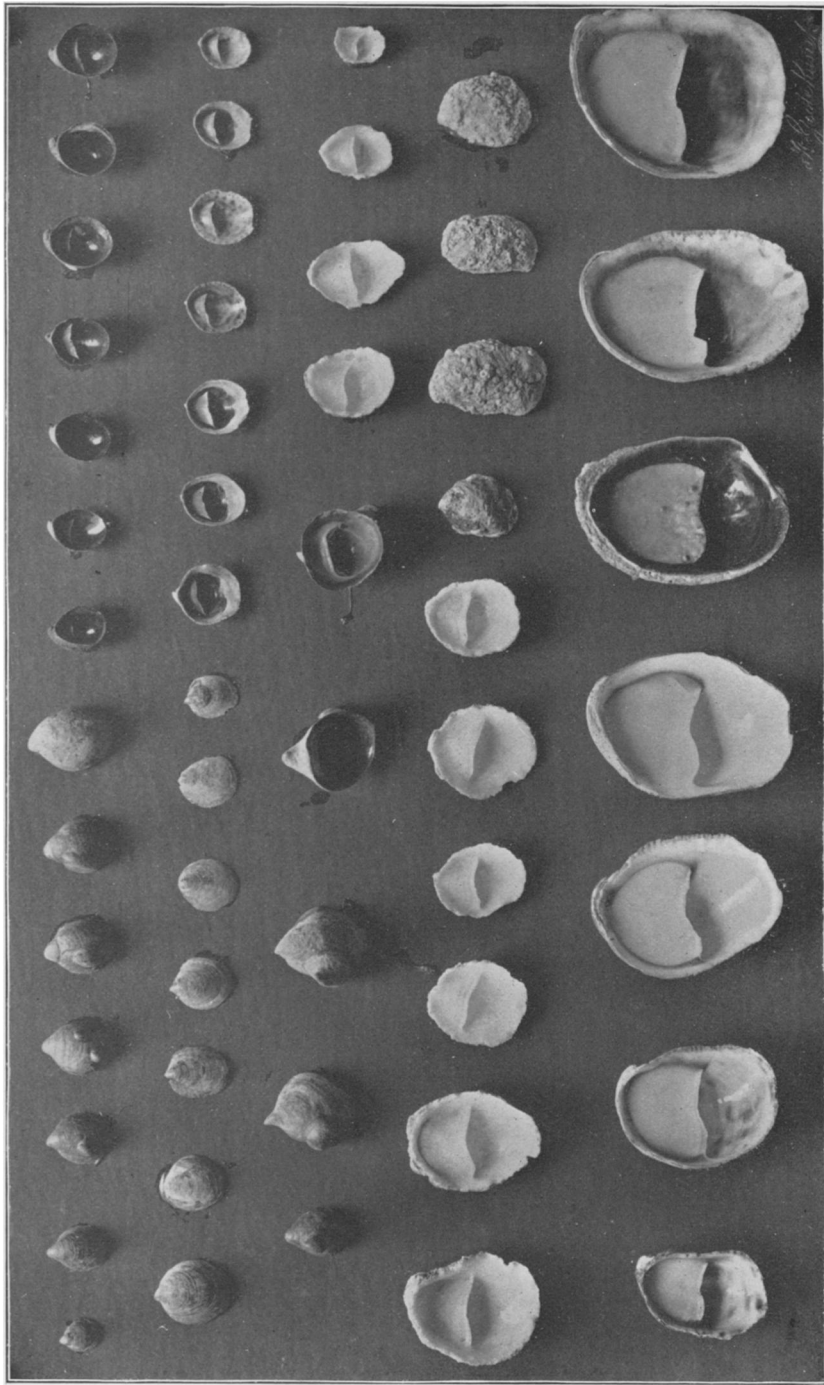
- Plate XXI. Row 1. *C. convexa* from exterior of *Illyonassa*. The shells are deeply pigmented and highly arched; 3d to 6th show males attached.
Row 2. *C. convexa* (*C. glauca* Say) from flat surfaces, some from exterior of oyster shells. The shells are unusually flat and broad, and those from the oyster shells are light in color and mottled with brown spots.
Row 3. First five shells are *C. adunca*, all with males attached. Remainder of row and all of
Row 4. *C. navicelloides*; many of the shells irregular in shape.
Row 5. *C. fornicata*; various sizes, shapes and colors.
- Plate XXII. All shells on this plate are of *C. plana*.
Row 1. Interior views of shells of very different shapes, due to the characters of the surfaces of attachment.
Row 2. Exterior views of same.

⁸ Embryology of *Crepidula*, Jour. Morph., Vol. XIII.

Row 3. Exterior views of dwarfs (mature females) from interior of *Illyonassa* and *Littorina* shells inhabited by the small hermit crab.

Row 4. Interior views of same. Last five shells in row males and immature forms of dwarfs.

Plate XXIII. All shells shown are those of *C. plana*.
Row 1. Immature forms; not differentiated sexually.
Row 2. Mature males.
Row 3. First six, mature males; seventh to tenth, forms intermediate between males and females; last shell in row immature female.
Row 4. Mature females; a few with males attached.



CONKLIN ON CREPIDULA.



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